THE NATURE OF NERVE CONDUCTION IN CASSIOPEA

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The experimental side of this research was conducted at the Marine Laboratory of the Carnegie Institution at Tortugas, Florida, and the kymograph records were studied under most advantageous surroundings kindly offered in Guyot Hall, Princeton University, by Profs. Edwin G. Conklin, Ulric Dahlgren, and Louis R. Cary. Ring-shaped strips of subumbrella tissue of the scyphomedusa *Cassiopea xamachana* were cut

TABLE I

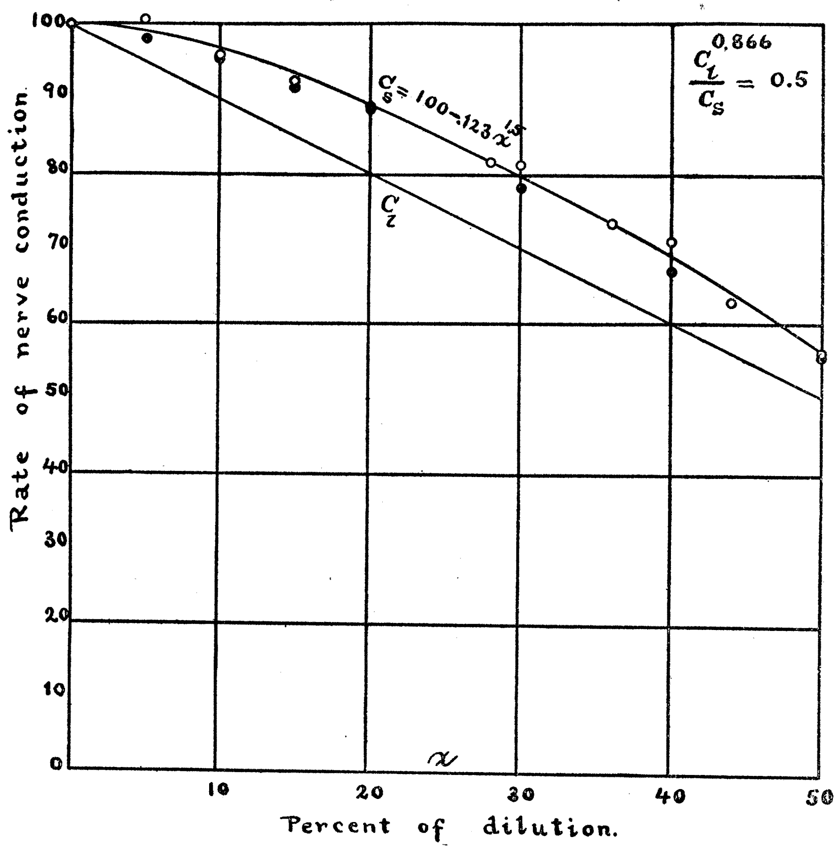
COMPOSITION OF THE SOLUTION	AVERAGE RATE OF NERVE CONDUCTION IN SEA WATER DILUTED WITH DISTILLED WATER	AVERAGE RATE OF NERVE CONDUCTION IN SEA WATER DILUTED WITH 0.415 MOLECULAR $MgCl_2$	RATE CALCULATED FROM THE FORMULA $C_s = 100 - 0.123\,x^{1.5}$ WHERE C_s IS THE RATE CORRESPONDING TO ANY PERCENT OF DILUENT, x
Natural sea water..................	100.0	100.0	100.00
95.0 volumes sea water + 5 of diluent	100.5 ± 0.67	97.9 ± 0.60	98.63
90.0 " " + 10 "	95.89 ± 0.825	95.3 ± 1.23	96.11
85.0 " " + 15 "	92.3 ± 1.21	91.6 ± 0.75	92.85
80.0 " " + 20 "	88.3 ± 1.19	88.9 ± 1.20	89.00
72.0 " " + 28 "	81.94 ± 0.48		81.78
70.0 " " + 30 "	81.4 ± 1.49	78.1 ± 0.74	79.79
64.0 " " + 36 "	73.91 ± 0.68		73.43
60.0 " " + 40 "	71.1 ± 1.29	67.2 ± 0.65	68.88
56.0 " " + 44 "	64.55 ± 1.26		64.10
50.0 " " + 50 "	56.31 ± 1.62	55.4 ± 0.76	56.50
33.3 " " + 66.7 "	29.0 ± 1		33.05

so as to remove the marginal sense organs, thus paralyzing the ring. Then a contraction wave was entrapped in the circuit, and the ring was placed in sea water diluted either with distilled water, or with 0.415 molecular magnesium chloride. The decline in rate was almost identical in similar concentrations of both these solutions although the magnesium appears to be slightly more depressant than the distilled water.

Experiments made in 1913 showed that the decline in rate of nerve conduction is the same in sea water diluted with 0.9 molecular dextrose as in sea water diluted with distilled water, and thus it is evident that down to 50% concentration the decline in rate is due solely to the change in concentration of the cations sodium, calcium and potassium, and not to the reduced osmotic pressure, or to magnesium.

Table I shows the results of the observations of 1914, the probable errors being expressed as ± following the mean. Thus 100.5 ± 0.67 means that the average rate was 100.5 with a probable error of ± 0.67.

As the table is based upon 373 observations, the probable errors are on the whole low for physiological results and are not greater than 1.62%.



If C_s be the velocity of nerve conduction corresponding to any percentage of diluent x (thus in 75 volumes of sea water mixed with 25 volumes of distilled water, $x = 25$), then

$$C_s = 100 - 0.123\ x^{1.5}$$

But a more interesting relation exists which may throw new light upon the nature of nerve conduction, for it appears that the curve representing the velocity of nerve conduction is identical in form with that for adsorption.

Past experiments show that the rate of nerve conduction in *Cassiopea* depends upon the concentration of the cations sodium, calcium, and potassium, and not upon osmotic pressure or upon magnesium.[4] This

being so, and if nerve conduction be a chemical phenomenon, we should expect according to Wilhelmy's law that its rate would be proportional to the concentration of these three cations which take part in the reaction.

Thus if the particles of the colloidal nerve substance carry a negative charge they would attract these positive cations to their surfaces, in accordance with the well known formula $C_s = \beta C_l^{1/p}$ where C_s is the concentration of the sodium, calcium, and potassium cations in the colloidal nerve substance; C_l is the concentration of these cations in the surrounding sea water; and β and p are constants.

TABLE II

COMPOSITION OF THE SOLUTION	C_l RELATIVE CONCENTRATION OF THE CATIONS $\dot{Na}$, $\ddot{Ca}$, AND $\dot{K}$ IN THE DILUTED SEA WATER	C_s OBSERVED RATE OF NERVE CONDUCTION	$\frac{C_l^{0.866}}{C_s}$
Natural sea water....	100.0	100.00	
95.0 volumes of sea water + 5.0 of distilled water....	95.2	100.50	0.51
90.0 " " + 10.0 " "	90.5	95.89	0.51
85.0 " " + 15.0 " "	85.5	92.30	0.51
80.0 " " + 20.0 " "	80.8	88.30	0.50
72.0 " " + 28.0 " "	73.3	81.94	0.50
70.0 " " + 30.0 " "	71.4	81.40	0.49
64.0 " " + 36.0 " "	66.0	73.91	0.52
60.0 " " + 40.0 " "	62.2	71.10	0.50
56.0 " " + 44.0 " "	58.4	64.55	0.52
50.0 " " + 50.0 " "	52.8	56.31	0.55
33.3 " " + 66.7 " "	37.5	29.00	0.79*

* Injurious osmotic effects are produced by this extreme dilution.

As appears in table II the conditions of this hypothesis are fulfilled down to concentrations of sea water diluted with an equal volume of distilled water, the exact formula being

$$C_s = 2.0\, C_l^{\frac{1}{1.154}}. \quad \text{Hence } \frac{C_l^{0.866}}{C_s} = 0.5.$$

As the rate of nerve conduction must according to Wilhelmy's law be proportional to C_s, we may substitute it for C_s.

Thus apparently the velocity of nerve conduction is proportional to the degree of concentration of the cations sodium, calcium and potassium which are drawn from the surrounding sea water and concentrated by adsorption upon the surface of some undetermined negatively charged colloidal particles of the nerve. In fact the nerve stimulus which produces pulsation appears to be conducted by these cations themselves, taking part in some reversible chemical reaction accelerated by an enzyme.

The presence of these positively charged cations must tend to reduce the surface tension of the colloidal particles, and with it the negative potential. In fact the sudden augmentation of the negative charge upon any one of the colloidal particles would attract other positive cations from the surfaces of neighboring particles and initiate a local negative potential which would travel through the nerve.

It is more probable however that, as the velocity of nerve conduction is proportional to the degree of concentration of the adsorbed sodium, calcium, and potassium cations, these cations themselves initiate the reaction and form some reversible chemical compound with some proteid substance, thus temporarily neutralizing their positive charges and unmasking the negative charges upon the colloidal particles to the surfaces of which they were attracted by adsorption.

These various hypotheses are suggested not so much as possible explanations of the phenomenon of nerve conduction, but more to stimulate interest in the problem and to suggest directions for further research. It is perhaps a step in advance to know that, whatever its precise nature, nerve conduction is some chemical reaction involving the adsorbed sodium, calcium, and potassium cations, and thus its rate is proportional to the concentration of these adsorbed ions.

The almost instantaneous recovery observed when the medusa is taken out of dilute sea water or magnesium solutions and replaced in natural sea water, and the very short time required to assume a constant rate of nerve conduction when the medusa is placed in concentrated or diluted sea water is readily explained by the theory that nerve conduction is dependent upon the adsorption of the conducting cations by negatively charged colloidal particles and is thus a surface effect.

The previous work of Meltzer and Auer, Mines, and Mayer has shown that it is probable that the calcium enters into combination with the sodium, possibly forming an ion-proteid. It now seems probable that this intimate association between calcium and sodium takes place upon the surfaces of the particles of the colloidal nerve fluid or some other colloidal elements of the nerve.

In this brief summary it may be inexpedient to review the literature of the subject, but the bearing of this research upon the observations of Macallum, 1913, upon changes in surface tension in active cell membranes, and of Tashiro, 1914, upon the production of carbon dioxide by active nerves (see these *Proceedings*, **1, 110**), is apparent, and the contention of R. S. Lillie that cell surfaces play the important rôle in stimulation is strongly supported.

It is a great pleasure to express my sense of indebtedness to Dr. E. Newton Harvey, Prof. George Augustus Hulett, and Dr. Stewart Paton of Princeton University for timely advice and aid.

A NEW CANONICAL FORM OF THE ELLIPTIC INTEGRAL

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The elliptic norm curve E_n in space S_{n-1} admits a group G_{2n^2} of collineations, and in fact there is a single infinity of such curves which admit the same group. A particular E_n of the family is distinguished by a value of the parameter τ, itself an elliptic modular function defined by the modular group congruent to identity (mod n).

In the group G_{2n^2} there are certain involutory collineations with two fixed spaces. If E_n is projected from one fixed space upon the other, a family of rational curves R_m mapping the family of E_n's, is obtained. The quadratic irrationality separating involutory points on E_n involves the modulus τ and the parameter t of the R_m. When the genus of the modular group is zero and $n = 3, 4, 5$, the irrationality can be used to define the elliptic parameter

$$u_1 = \int \frac{(t\,dt)}{(t\,\tau)\,\alpha_\tau^{r-3}\,\alpha_t^3},$$

where α_t^r is the tetrahedral, octahedral, or icosahedral form. This is in contrast to Klein's form[1] as developed by Bianchi,[2] for there the normal elliptic integral is a rational curvilinear integral along an elliptic curve.

A comparison of the two integrals is more illuminating if it is carried out for a special case. Let E_n be E_5 in S_4. In Bianchi's notation the five quadrics having E_5 as their common intersection are

$$\varphi_i : a\,x_i^2 + a^2\,x_{i+2}\,x_{i+3} - x_{i+1}\,x_{i+4} = 0,\ (x_{i+5} \equiv x_i),\ (i = 0, \cdots 4),$$

where a is the modulus. If a transformation of coordinates is made in order to bring into evidence the fixed spaces of the involutory collineation used in the projection, then the icosahedral form which appears in the irrationality is

$$\alpha_t^{12} = t_1\,t_2\,(t_1^{10} + 11\,t_1^5\,t_2^5 - t_2^{10}).$$

The integral u_1 involving $\tau = a$ explicitly in a rather simple form is uniquely defined. Moreover it is invariant under all cogredient trans-